A CASE OF DUPLEX CONVERGENT RESEMBLANCE IN AUSTRALIAN MAMMALS, WITH A REVIEW OF SOME ASPECTS OF THE MORPHOLOGY OF PHASCOGALE (ANTECHINUS) SWAINSONI WATERHOUSE AND PHASCOGALE (ANTECHINUS) FLAVIPES WATERHOUSE

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SUMMARY

The distribution and status of *Phascogale* (*Antechinus*) *flavipes* and *Ph.* (*Antechinus*) *swainsoni* in South Australia is dealt with and some differential characters of the two species are reviewed in series.

A new subspecies of *Ph. swainsoni* is defined in the lower south-eastern district of South Australia and adjoining parts of Victoria.

Dark coloured variants of both species are produced on invasion of wet areas of heavy stringybark forest in south-west Victoria.

Both rufescent and fuliginous phases of both species form strikingly similar synchromatic pairs, the former being allopatric, the latter sympatric.

In 1924, Oldfield Thomas first drew attention to the remarkable convergent resemblance in external characters, which existed between sympatric forms of these two marsupials in northern New South Wales. The purpose of the present note is to record a similar circumstance involving the same two species, still occurring sympatrically in a restricted area west of Heathmere in south-western Victoria. This locality is distant nearly 1,000 miles along the axis of distribution from the northern site, and is near the western limit of the range of *Ph. swainsoni*.

The case is more complicated than the New South Wales one, since two forms of each species are involved; the one normal and widespread, the other variant and localized. The aberrant forms, like those dealt with by Thomas, show a departure from a comparatively richly coloured pelage to a dull fuliginous one, together with certain minor structural changes, to be noted. In working out the identity of the two, which are most intriguingly disguised, I have found it necessary to review a considerable quantity of material representing both species, drawn from other areas than that which produced the variants, in order to establish what might safely be considered as the normal range of variation, and to clarify the differences which may be relied on as critical. Incidentally, a new subspecies of *Ph. swainsoni* is defined in South Australia where the species was doubtfully recorded,* and the status and distribution of both species in that State, which has been obscure, is discussed.

The interrelation of the synchromatic pairs may be summarized thus:

A. RUFESCENT PHASES: ALLOPATRIC

Form 1. *Ph. flavipes rufogaster* Gray.
Form 2. *Ph. swainsoni maritima* subsp. nov.

B. FULIGINOUS PHASES: SYMPATRIC

Form 3. *Ph. flavipes rufogaster*, Heathmere variant.
Form 4. *Ph. swainsoni maritima*, Heathmere variant.

* The name was included in a list of South Australian mammals in Harcus's "South Australia" in 1876, but no material in support of this record has been traced.

The area of occurrence of the variant phase of both species lies in the county of Normanby and stretches north-west from the basalt formations of the Mt. Clay Range as a gently sloping, low-lying plain, to the limestone gorges of the

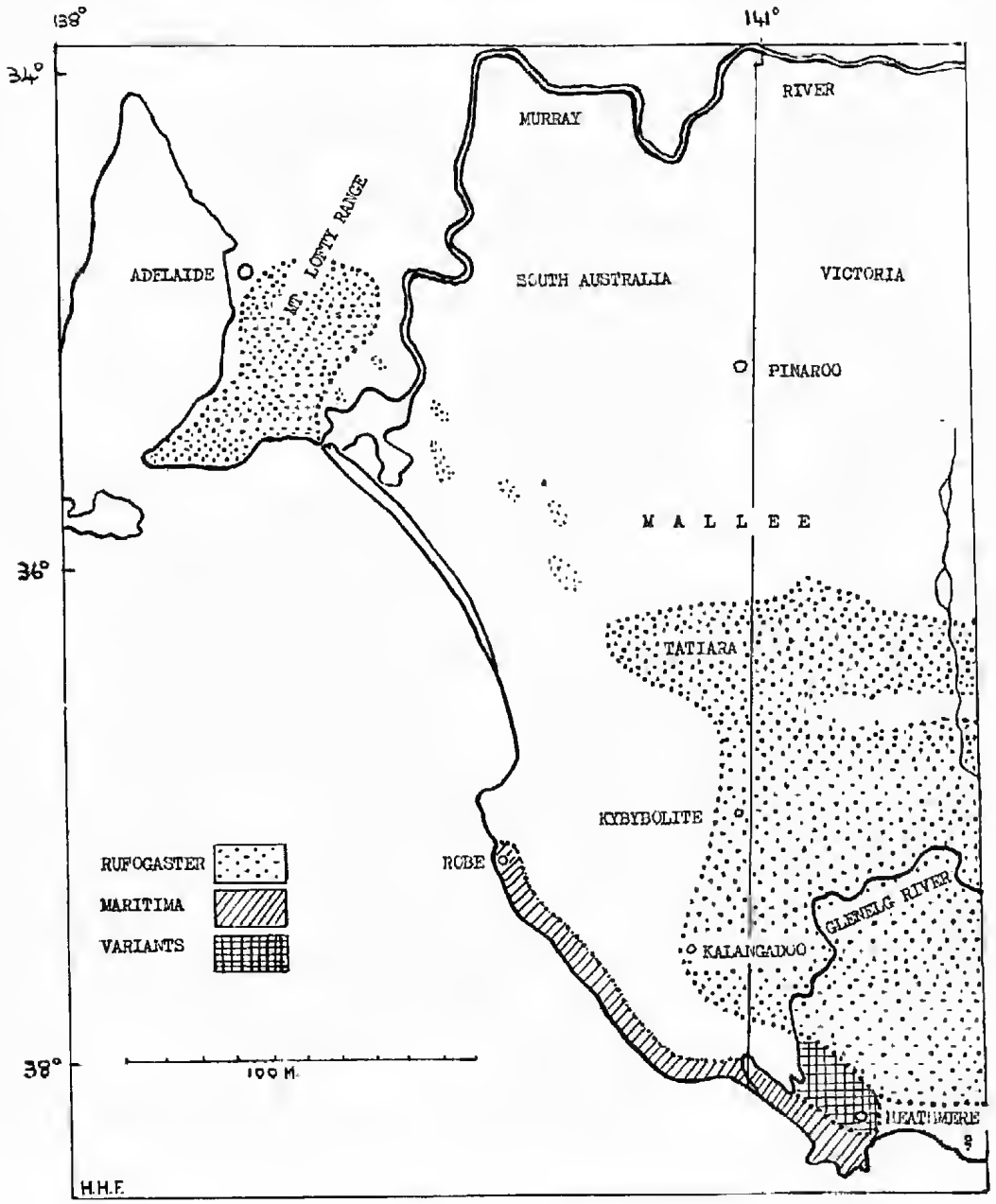

Fig. 1.

Map of south-eastern portion of South Australia and adjoining areas of Victoria, showing main lines of distribution of *Phascogale (Antechinus) flavipes rufogaster* and *Ph. (Antechinus) swainsoni maritima* subsp. nov.

Glenelg River near its great western bend, about 15 miles from the South Australian border. The average height above sea level is no more than 150

feet, the rainfall reaches 60 inches, and much of it is strongly subject to maritime influences from the nearby coasts of Discovery and Portland Bays. The town of Portland, not shown on the map (Fig. 1), is approximately 10 miles south of Heathmere.

Until recent years the greater part of the area was a dense and almost virgin forest of *Eucalyptus capitellata* and *E. obliqua* interspersed with small, swampy heaths where Leptospermums and Melaleucas form nearly impenetrable thickets. The trees occur in massed stands and are often of great size and consisting entirely of grey rough-barked species, form—especially when swept by sea fogs as they frequently are—one of the most sombre of Australian forest landscapes.

The region is rich in relict forms, and amongst mammals which have found sanctuary here from the extirpation which has fallen upon them in contiguous tracts, may be mentioned *Potorous tridactylus*, *Petaurus australis*, *Phascolarctos cinereus*, and *Dasyurus maculatus*. These are still extant. *Sarcophilus harrisi* is believed extinct here, but almost certainly persisted immediately prior to European occupation.

Form 1—*Phascogale flavipes rufogaster* Gray.

Status and distribution.—The species occurs today in two widely separated districts of South Australia: 1. The southern section of the Mount Lofty Range and its outlying foothills; here the country chiefly occupied is on the lower drier slopes in areas of more or less open park-like aspect where the dominant tree is *Eucalyptus leucoxylon* sometimes fringed with *E. odorata*. The most northerly spontaneous occurrence of which I have knowledge is at Mt. Torrens, east of Adelaide, but 40 years ago the animal was intentionally introduced into the Barossa district, 20 miles north of this, and it may be expected to occur sporadically in the north Mt. Lofty Range. 2. The border areas of the south-eastern district from the Tatiara to Kalangadoo; here somewhat similar open forests of *E. leucoxylon* and *E. rostrata* (=*camaldulensis*) occur, though at lower elevations and on extensive plains without vertical relief, and extend east, deep into Victorian territory. The interval of 150 miles between these two forest areas is occupied by an expanse of mallee scrub which, together with the River Murray, virtually isolates the two *flavipes* populations from one another or at least limits them to a very tenuous connection through a chain of widely separated oases of bigger timber. But in spite of this, there is little evidence of differentiation and they are here treated as a subspecifically homogeneous unit, extending at least to the eastern slopes of the Grampian Range in Victoria, which yielded the most easterly of the specimens examined.

There are no records available here, either to the west or north-east, to suggest that *Ph. flavipes rufogaster* has been in contact in recent time, either with *Ph. flavipes leucogaster* of Western Australia or with the populations of the eastern States, except by this south-eastern route.

Phascogale flavipes is a comparatively rare animal in South Australia—much more so than in Victoria or New South Wales—but has nevertheless a firm hold on its ground. This is the more remarkable since its habitats lie in districts which have been farmed for a century or more, and which for the latter half of that time, have been heavily infested by the European fox.

When local circumstances are favourable it is capable of building up considerable density of population in restricted areas. This was so, for instance, in 1932 on the Coohawang Creek at the southern extremity of the Mt. Lofty Range, where it became so numerous that in a few weeks over 20 were taken in live traps in an area of a few acres. The animal was practically unknown on this creek before that time and the cause of its sudden increase was traced to an equally sudden expansion of rabbit trapping, which led to the accumu-

lation of carcasses in dumps, and the provision of both flesh and insect larvae on a lavish scale.

Similar increases have been noted in the vicinity of bee hives which are sometimes selected as nesting sites, but whether the attraction here lies in the insects and their larvae, or the honey, is uncertain; in winter it is possible that the higher temperature of the hives may draw it thither, as G. G. Goodwin (1935) suggests in the case of *Peromyscus leucopus* which has a similar habit. Standard accounts of the animal, such as that of Thomas (1888), describe it as strictly arboreal and insectivorous, but this needs much qualification. It is no doubt capable of a strictly arboreal life, and is almost confined to forested tracts, but nevertheless spends much time on the ground and feeds very largely there. Besides hollow limbs of standing trees, it shelters and nests in fallen logs, rock crevices and crannies in the roofs and walls of caves. On the south-eastern foothills of the Mt. Lofty Range, where the terrain is often rock strewn, the north country practice of fencing fields with stone walls was early introduced by English settlers, and in these walls *Ph. flavipes* finds a secure retreat. In the wild, it is known to kill and eat murids as well as insects and their larvae, and in captivity devours beef ravenously.

On reproduction, the data available is scanty; the uterine condition has not been investigated, but mammary activity in females has been noted from August till November, and in captivity wild caught examples showed marked intersexual activity in June and July. Two females were carrying large litters of sucklings—the one, 10 at a 13 mm. stage (undated) and the other 9 at 7 mm. in August. The sex ratio in the determinable portion of the series examined is 17 ♀ and 24 ♂.

Of ecto parasites, a sparse infestation of a tick occurs, but *laelaps*, known from the related genus *Sminthopsis* of the same areas, has not been noted.

The long persistence of so primitive a form in settled districts where it is subject to many adverse influences — a persistence perhaps now approaching equilibrium — is a notable thing, where so many more specialized mammals have been swept away by the changing conditions.

External characters.—The following account is based upon the examination of a series of 52 individuals. As an excellent general description of the animal by Professor Wood Jones (1923) is available, attention is concentrated on characters which have been somewhat obscure or which serve to distinguish it from *Ph. swainsoni*.

The *head* is broad and deep and massive, with a short conical muzzle. All facial vibrissae are very strongly developed. Ear long and conspicuous; the pinna thin in substance and with a somewhat peaked apex and a notched or sinuous posterior margin.

The *manus* is comparatively broad and stout; in the largest males its approximate dimensions are: Length from base of carpal pads to apical pads, 11 mm.; breadth across base of digits, 7 mm.; length of 3rd digit, 4 mm. The claws are yellowish white in colour, much flattened from side to side and comparatively weak—in wild caught males they attain 3·5 mm., but this may be much increased in captivity. The palms are flesh coloured and conspicuously granular.

The pads vary within wide limits as to detailed shape and relative size. The outer metacarpal (hypothenar) is generally a broad inverted U, blunt at the apex but the remaining pads are much narrower, long oval or slightly piriform. The outer metacarpal is always much the largest, and the most frequent size relation is, outer metacarpal > inner metacarpal > 4th interdigital > 3rd — 2nd > 1st; but numerous variants occur. The 4th (outer) interdigital is frequently broader than its fellows and otherwise modified in shape. The condition illustrated by Wood Jones, in which the inner metacarpal is aborted or fused with the 1st interdigital (pollical), is evidently rare and is not repre-

sented in the present series where a well separated condition is invariable and is usually emphasised by differences in shape. All pads are striate—the outer metacarpal radially, the rest transversely.

The *pes* in largest males attains a length of 21·5 mm. and breadth 6·5 mm.; the length of 3rd digit 6 mm., its nail 3·5 mm., and the hallux 3·5 mm. The plantar surface is uniformly granular and flesh coloured like the manus and all pads are transversely striate. The pads are even more variable than those of the manus. The inner metatarsal is invariably the largest and is usually a shallow crescent with the concavity lateral. The outer metatarsal is also occasionally crescentic, with its curvature opposed to that of the inner, but is more often a long oval or club-shaped structure, with its greatest width distal. Both metatarsal pads are commonly rotated outwards distally from the long axis of the foot. The interdigitals are long ovals or narrow piriform, and their size relations are different from those of the manus, the 2nd and 3rd usually exceeding the 1st and 4th, the latter frequently being the smallest pad and equally subject to broadening and aberrations of shape. A frequent size sequence is: Inner metatarsal > outer metatarsal > 2nd interdigital = 3rd > 1st > 4th, but in a considerable minority the median interdigitals exceed the outer metatarsals. Complete separation of the inner metatarsal and the 1st interdigital (hallucal) is normal, the fusion of the two occurring in only 11 per cent. (approx.) of the series studied.

The series is somewhat deficient in lactating females and in the quiescent condition a count of mammary nipples is often unsatisfactory. Of the 5 best examples, 4 possess 10 nipples and the 5th, 9; all functional.

Dimensions.—The following figures give in turn the range, approx. mean and percentage relation of mean to the head and body length, of 14 males and 10 females, free from obvious immaturity. The ear measurement is from the inferior tragoid notch and is not comparable with earlier published data: Head and body ♂ 112-133 (120); ♀ 102-120 (109). Tail ♂ 86-115 (102), 85 per cent.; ♀ 80-95 (88), 81 per cent. Pes ♂ 18-21·5 (20), 17 per cent.; ♀ 18-19 (18) 16·5 per cent. Ear ♂ 16-20 (18), 15 per cent.; ♀ 15-18 (17), 15·5 per cent.

Two fresh killed males of medium size weighed 49 and 44 grammes respectively.

Pelage.—The chief points of interest here are that the head and foreparts of the dorsum are contrasted both in texture and colour with the hinder back; the former being usually crisp and short and a cold, grizzled iron grey, the latter variably suffused with rufous but still grizzled with black. On the lateral and midventral areas, this colour appears in undiluted form often as a rich, almost orange tan, between Ridgway's ochraceous orange and ochraceous tawny, and forming a broad belt separating much paler yellow buff gular and inguinal areas. The body hairs are everywhere dark plumbeous at base. Very characteristic are the supra and infra orbital crescents of light buff, strongly contrasted with other facial areas, and the tufts of undiluted buff hair at the base of the ear backs, which are tan or buff in contrast to the grey head. The dorsum of manus and pes are buff or rich tan, never grizzled with a darker element. The tail (unless it be in aged or bleached pelage) is decidedly bicolour—grizzled black and buff dorsally, darkening rapidly to pure black for the apical third and buff or tan below; the caudal hairing is dense and relatively coarse, hiding the epidermal scales on the dorsum at least, and often forming an incipient brush terminally.

The skull and dentition (Pl. 1, figs. e, f, g, h).—The skull characters and dentition while in general agreement, show some minor deviations from the account of Thomas (1888), which was founded on a composite of 2 races (as now considered). However, variation in South Australia is considerable, even

across quite insignificant geographical intervals, and no attempt will be made here at a racial definition of *rufogaster* under these heads.

At species level, the main points of differential value, which are confirmed in the present series, are as follows. The skull is stoutly built, broad zygomatically and with a short conical rostrum. The interorbital region is broad, but its margins appreciably arcuate. The anterior palatal foramina are narrow and crescentic, short but variably so, extending usually to the posterior base of the canine but sometimes to the middle of P^1. Posterior palatal bridge more than half the width of the vacuities. Coronoid process tall and narrow. Bullae relatively large.

In the dentition I^1 is strongly differentiated from I^{2-4}, with at least twice the bulk and vertical projection; distinctly proodont and separated from I^2 by an evident gap; $I^2 > I^3 > I^4$, the inequality slight but appreciable, especially in section as seen from the palate (not subequal as per Thomas). $P^1 > P^3 > P^2$, but the proportion variable; P^1 and P^2 sometimes subequal; P^1 always much larger, sometimes 2 to 3 times the bulk of P^2. In the anteroposterior length of the buccal wall, $M^1 >$ or $= M^2 > M^3 > M^4$. In the lower incisors $I_1 > I_2 > I_3$, but I_1 and I_2 may be subequal and I_1 sometimes much longer than either. In the lower premolars $P_3 > P_1 > P_4$ and in antero-posterior length $M_3 >$ or $= M_2 > M_4 > M_1$.

The following dimensions are derived from 9 adult skulls, 5 ♂, 4 ♀. Basal length ♂ 27·3-29·9 (28·2); ♀ 26·1-27·6 (26·8). Greatest breadth ♂ 16·3-20·0 (17·9); ♀ 16·0-17·3 (16·6). Nasals length ♂ 10·4-11·5 (10·9); ♀ 10·0-10·5 (10·3). Nasals greatest breadth ♂ 3·4-5·0 (4·3); ♀ 3·2-4·6 (3·9). Intertemporal breadth ♂ 6·3-6·7 (6·6); ♀ 6·3-6·6 (6·5). Palate length ♂ 15·7-17·4 (16·3); ♀ 15·3-15·8 (15·6). Palate breadth outside M^3 ♂ 10·0-11·2 (10·5); ♀ 9·5-10·3 (9·9). Anterior palatal foramina ♂ 2·6-3·1 (2·8); ♀ 2·5-2·8 (2·6). Ms^{1-3} ♂ 6·0-6·4 (6·1); ♀ 5·8-6·0 (5·9).

Tate (1947a) implies that the molar rows diminish in a metrical cline from North Queensland coastwise to Western Australia, but this seems to be an oversimplification, as the *rufogaster* figures are frequently higher than those recorded for New South Wales.

Form 3.—*The Heathmere variant of Ph. flavipes rufogaster*

Differing from *Ph. f. rufogaster* (supra), of which it is obviously a derivative, chiefly in the almost complete suppression of rufous and fulvous tones in the pelage. This is rather loose and lax and the antero-posterior differentiation both of texture and colour, is largely lost. General dorsal colour a dull scarcely grizzled brown, about Ridgway's mummy brown; ventrally a paler grey brown on gular, sternal and inguinal areas but on the mid-belly belted across by a broad area of dorsal colour, the zoning exactly as in *rufogaster*. Ear backs drab, scarcely contrasted with the head and no contrasting outer basal tufts and the orbital crescents obscure. Manus and pes pale drab. Tail dull buffy at base dorsally, the rest drab, ticked with black and darkening but slightly towards the apex; drab below, the bicolour character much reduced.

In the pes the inner metatarsal and hallucal pads are fused. Morphologically there is complete identity in cranial and dental characters with *rufogaster*, but metrically the two examined give values above the means for the intertemporal breadth and width of ascending process, and below the mean for the bulla and molar rows. These differences while probably of no systematic significance, serve to heighten the convergent similarity to *swainsoni* of the same district.

This form is obviously a southern analogue of *Ph. flavipes adusta* Thomas (1923) from North Queensland and of *Ph. flavipes unicolor* Gould (1854) of northern New South Wales in which the darkening and equalizing of the colour

scheme have been carried a stage further. Le Souef and Burrell (1926) record a similar variant from eastern New South Wales.

Ph. swainsoni swainsoni Waterhouse

In testing the characters of this species I have relied mainly on a series of 16 from Cradle Valley, Tasmania, at an altitude of 3,000 feet in a subalpine climate. How far this material may be taken as typical of the species in the island as a whole is uncertain, for while there is general agreement with Thomas' account (1888), the skull from the Tasman Peninsula measured by him indicates a much larger animal than occurs in this collection. My own sojourn in Cradle Valley was limited to midsummer, when the species was locally scarce, but in winter when much of the valley is snow-bound, it concentrates in sheltered spots and may invade camps and even homesteads. I am much indebted to the late Gustav Weindorfer, a well-known naturalist long resident on this interesting site, for the series reviewed, part of it being taken actually within his chalet of Waldheim.

Approximately half the series is subadult and the sex ratio is 13 ♂ and 3 ♀: it yields no data on the incidence of reproduction.

External characters (the comparison throughout is with *Ph. flavipes rufogaster*).—The *head* is shallow and narrow and somewhat shrew-like, with a long, narrow muzzle. The ear short and broad: the structural features of the conch similar but with the posterior margin of the pinna more rounded and less sinuous. The ear projects less from the head—a characteristic which tends to be obscured by the conventional measurement taken from the inferior tragoid notch. The vibrissae are as long, but weaker.

In the *manus*, which yields similar measurements, the most conspicuous difference is in the claws, which are generally both longer and stronger (reaching 4-5 mm. in large males) and less flattened in section. The latter is the better distinction, the size difference being less constant than is believed, *rufogaster* showing some adaptive variation in this feature. The palm is dusky pink, the colour variable, but always darker; it is variably granulated, usually more sparsely than shown in Fig. 1, and the individual granules are often darker than the interstices. The outer metacarpal pad is variable, but often assumes an inverted heart shape, more acute at the apex than in *flavipes* and with the inner margin shorter or incomplete towards the base. A more marked distinction is provided by the complete fusion of the inner metacarpal with the 1st interdigital in 95 per cent. of cases; the interdigitals tend to be shorter and rounder than in *flavipes*.

The dimensions of the pes are not significantly different from those of *rufogaster*; in plantar aspect, however, the foot tapers more rapidly to the heel giving a false impression of greater breadth and having a more marked expansion on the outer margin, opposite the outer metatarsal pad; pigmentation and granules as in the manus. The foot pads are similar but are equally variable. The outer metatarsal, however, is considerably larger, sometimes equalling the inner (which is rarely so in *rufogaster*) and always exceeds the interdigitals; the inner metatarsal and 4th interdigital are shorter. The most frequent size sequence is: Inner metatarsal > outer metatarsal > 2nd interdigital > 1st > 3rd > 4th.

The condition of the hallucal pad is a matter of special interest, as its more or less complete fusion with the inner metatarsal has been claimed as a specific character of *swainsoni* distinguishing it from *flavipes*. In the series examined, however, only 4 (25 per cent.) show complete fusion and in these the junction of the original elements is always made obvious by a constriction at the site. In the remaining 75 per cent., the majority show separation as complete as in *flavipes rufogaster*, a low level gap of at least 1 mm. occurring between the two. Somewhat unexpectedly the fused condition proves to be 3 times as

frequent in subadults as in adults. The conjoined structure usually assumes the form of an open sigmoid curve, but may be almost straight as in Fig. 2.

Dimensions.—The following figures give in turn the range, approximate mean and percentage relation of the mean to head and body length of 7 males and 1 female, all adult: Head and body ♂ 110-135 (118); ♀ (103). Tail ♂ 97-110 (101), 86 per cent.; ♀ (86), 83 per cent. Pes ♂ 20-21 (20·6), 17·5 per cent.; ♀ (18), 17·5 per cent. Ear ♂ 15-17 (15·5), 13 per cent.; ♀ (14), 13·6 per cent., and similarly in 6 males and 1 female subadult: head and body ♂ 86-100 (92); ♀ (98). Tail ♂ 82-90 (87), 95 per cent.; ♀ (80), 82 per cent. Pes ♂ 18-20 (19), 20·7 per cent.; ♀ (18), 18·3 per cent. Ear ♂ 14-16 (14·5), 15·8 per cent.; ♀ (14), 15·3 per cent.

As compared with *flavipes rufogaster* the chief difference is in the ear, which (as measured from the lower tragoid notch) is about 14 per cent. shorter in *swainsoni*. The figures for the subadults are of interest as stressing the relatively greater development of appendages, ear, foot and tail all being relatively longer than in adults; the lag in the values for the female in this group is due to greater maturity.

In *pelage*, *Ph. swainsoni swainsoni* differs very markedly from *flavipes rufogaster*. The coat is soft and dense; dorsally there is little or no antero-posterior differentiation either in texture or colour, the latter being much darker, browner and less grizzled, near Ridgway's Vandyke brown but with glints of bronze. The ventrum is uniform greyish white with scarcely a tinge of buff and not much contrasted with the basal zone of slate. Orbital crescents absent. Ears concolorous with head. Manus and pes and tail are very dark brown, the latter only slightly darker at the apex and with little dorso-ventral contrast, and with thinner and shorter hairing.

The skull and dentition.—The skull is slenderly built, narrower zygomatically and with a long, weak rostrum—contrasted with the robust *flavipes* condition. The nasals and palate are longer and the anterior palatal foramina are nearly parallel-sided slits reaching to the back of the median premolar. The posterior palatal vacuities are also very long and narrow, reducing the width of the posterior palatal bar to less than half their length. The hamular processes of the pterygoids are remarkably long and attenuated and recurved and the bullae are smaller. The interorbital region is broader, with smooth, parallel sides. The mandible is slighter with a longer symphysis and a wider and shorter coronoid process.

The teeth throughout are slighter and narrower with higher and more discrete cusps. I^1 is less specialized than in *flavipes*; its length only twice I^2 and not strongly proodont and scarcely separated from I^2. The upper incisors flattened labio-lingually and subequal. The canines are both slighter and shorter, less vertical and with a more distinct posterior cuspule, and the lower tooth has a longer heel. The upper premolars are more widely spaced and the lower 4th premolar less reduced, leading to $P^3 > P^4 > P^1$ instead of $P^3 > P^1 > P^4$. The molar rows are shorter than in *flavipes rufogaster*, but overlapping the range of the Heathmere variants of that form.

The range of dimensions in two adult male skulls are as follows: Basal length 29·7-29·8; greatest breadth 16·1-16·7; nasals length 12·6-12·8; nasals greatest breadth 4·3-4·7; intertemporal breadth 7·9-8·2; palate length 17·7-17·8; palate breadth outside M^3 8·6-8·7; anterior palatal foramina 6·5-6·9; M^{1-3} 5·4-5·5.

FORM 2.—**Phascogale (Antechinus) swainsoni maritima** subsp. nov.
pls. 1 and 2.

A terminal race at sea level in lower South Australia from the south-west extremity of the range of the species. Separated from *Ph. swainsoni mimetes* Thomas (1924) (a highland race at 5,000 feet in northern New South Wales)

by a population of *Ph. swainsoni swainsoni* in south-eastern Victoria, of unknown extent, and differing from the latter (normally) in a richly rufescent dorsally bipartite colouration and in minor cranial changes towards *flavipes*; but producing also a dark pelage variant in the Heathmere district of Victoria. Distinguished from *mimetes* Thomas in its smaller size, shorter appendages, broader skull, and in the dominant phase, by a much richer colouration.

Plastic characters, generally as in the Tasmanian series reviewed (supra) but in the manus the fusion of the inner metacarpal and 1st interdigital pad is invariable and in the pes, the similar merging of the inner metatarsal and hallucal pad, occurs with more than twice the frequency (55 per cent.). The mammary nipples are 8 in number in the 2 examples where a count is possible and they are arranged as in *flavipes*; in this material they are not smaller than in the latter species, as found by Tate (1947b).

The range in dimensions, approx. mean and percentage relation to the head and body length in 4 males and 4 females (all adult) is: Head and body ♂ 118-135 (127); ♀ 107-117 (111); tail ♂ 92-107 (100), 78 per cent.; ♀ 72-83 (78), 70 per cent.; pes ♂ 20-21 (20·5), 16 per cent.; ♀ 17-18 (17·5), 16 per cent.; ear ♂ 14-15 (14), 11 per cent.; ♀ 14-15 (14), 13 per cent.

So far as the limited sample permits of conclusions, it would appear that the general body size is as great or slightly greater than in the Cradle Valley animal, and that tail, pes and ear are relatively slightly shorter; the female is shorter tailed than the male.

The skull is morphologically as in the Tasmanian race, but with a tendency towards laterality leading to metrical convergence in the direction of *flavipes*; the zygomatic and palatal breadth are increased; the length of rostrum, palate, and anterior palatal foramina, reduced, and the molar rows are longer and the individual molars slightly heavier.

Dimensions of 3 adult ♂ skulls are: Basal length 29·3-30·3 (29·8); greatest breadth 17·2-18·0 (17·5); nasals length 12·2-12·3 (12·2); nasals greatest breadth 4·6-5·0 (4·8); intertemporal breadth 7·7-8·0 (7·9); palate length 16·8-17·5 (17·1); palate breadth outside M^3 8·8-9·8 (9·3); anterior palatal foramina 3·0-5·5 (4·4); Ms^{1-3} 5·5-5·9 (5·7).

Pelage.—Texture moderate, less soft than in the Tasmanian animal; main pile about 10 mm. mid dorsally with contour hairs to 14 mm. General dorsal colour scarcely definably different from that of *Ph. flavipes rufogaster*; the head, nape and shoulders a cold, grizzled grey increasingly suffused posteriorly with rufous which may become very rich over the rump; sometimes deeper and more cupreous than in *rufogaster*, but often identical and similarly overlain with black contour hairs; markedly distinct from the brown tones of the typical race. Ventrum a uniform greyish white, but variably and sometimes strongly washed with yellow or buff and deep plumbeous for the basal 2/3. The lower lateral margins enriched with the dorsal rufous undiluted with black, but not crossing the mid-belly to give the belted pattern of *rufogaster*. The ear backs, lower course of fore and hind limb, and dorsum of manus and pes are uniform drab, or drab slightly ticked with dull grey or dull buff. The tail with short, fine hairs and untufted as in the typical race, but drab lightly grizzled with black above and scarcely bicolour dorsoventrally except at the apex where it may darken to bistre, or near black. Buff orbital crescents are conspicuously developed.

This phase occurs with essential uniformity in a narrow subcoastal zone extending from Robe in the south-eastern district of South Australia, south and east to Portland in Victoria, whence its eastern extension is not ascertained. The habitat is largely one of consolidated dunes, interspersed with swamps and fresh water lakes of considerable extent. It is for the most part well vegetated with low-growing species, but is often treeless and in marked ecological contrast to the forest habitats of *flavipes*.

Type.—M4985 of the South Australian Museum, from Port MacDonnell, south-east district of South Australia; collected by G. H. Tilley. Adult male in alcohol with skull extracted; 11 examples examined including field skins of the variants (infra) which are in my own collection.

FORM 4.—*The Heathmere Variant of Ph. swainsoni maritima.*

In South Australia *maritima*, as at present known, is virtually isolated from the *flavipes rufogaster* population of the Tatiara and Kalangadoo districts, but in Victoria a dark variant occurs sympatrically with that of *flavipes* in the same *E. obliqua* forests, west of Heathmere.

This is identical in all respects with the rufescent phase except in pelage colour, from which the rufous and fulvous elements are removed and replaced by drab and dull brown, exactly as in the *flavipes* variant; it may be regarded as a southern analogue of *Ph. s. mimetes* Thomas.

The resemblance of the two phases of the two species to one another is often extremely close, and it is possible to select synchromatic pairs of both colours from the four groups, which are so similar that they cannot be identified by an appeal to pelage characters alone. The situation is given added piquancy by the secondary convergence in cranial characters which although slight, adds a further element of confusion to any attempt at casual sorting. There is, of course, an ample residue of characters, especially in the dentition, which gives critical distinction as shown above, and in externals the forms of *swainsoni* can usually be recognised by the shorter ears and longer claws of the manus.

While the material examined of the normal or rufescent phases of the two species has been adequate for the purpose in hand, that relating to the fuliginous forms from the Heathmere district is scanty and limited to five specimens, two of *Ph. flavipes* and three of *Ph. swainsoni*, so that conclusions drawn from them are to some degree tentative. Nevertheless, the value of the evidence which they yield is much enhanced by the geographical abruptness of their appearance, by the absence of intergrades amongst them, and by the fact that two distinct species produce the same evidence in the same area.

The proper taxonomic treatment of such variants is a problem for the solution of which the available data is in general quite inadequate. Although it has long been known that similar modifications are produced by *flavipes* and *swainsoni* both in eastern Australia and in Tasmania, the extent to which these forms are geographically limited is obscure and in some cases it is not possible even to decide which is the normal phase and which the variant. The earlier recorded instances, notably those of Higgins and Petterd (1882-1883) in Tasmania were relegated, somewhat summarily perhaps, to the synonomy of the first described form, but later examples were treated as subspecies or even full species. It is possible that here chromatic dimorphism is involved, of a type common in Australian mammals, in which the same contrasting colour phases are produced at widely separated intervals in the range of the species and without obvious relation to local conditions.

In the present case the main facts are clear and point to quite different influences. Two homogeneous populations of distinct species, occupying well separated ranges, jointly invade a restricted area where the conditions are novel to both, and undergo there a strictly parallel modification of pelage. The superficial nature of the adaptive change suggests that a simple, possibly biochemical, factor is directly actuated by the change in external conditions.

How far these dark variants so produced may be regarded as genetically fixed and susceptible of treatment as subspecies, is more likely to be solved in

the laboratory than by field work. But from analogy it would seem almost certain that similar "pockets" of them, induced by similar microclimates are (or were) scattered over the very large areas of eastern Australia where the species occur. The dilemma seems to lead either to the recognition of a geographically unfixed "physiological race"—a conception still dubiously regarded in many quarters—or to the possible naming of a patchwork of isolated micro-subspecies, scarcely distinguishable except by the sites they occupy.

As much of theoretical interest may be obscured by the lavish use of subspecific names, it seems preferable at present to leave the fuliginous phases innominate and accept the unorthodoxy of the first expedient.

In conclusion, I wish to express my great obligation to Messrs. H. H. Finck of Heathmere and E. Peterson of Gorae, friends of long standing, whose frequent hospitality has enabled me to keep the local mammals under observation for many years.

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